

DISTRIBUTION OF PHOTOSYNTHETICALLY FIXED ^{14}C IN PERENNIAL PLANT SPECIES OF THE NORTHERN MOJAVE DESERT¹

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ABSTRACT.—The distribution of photosynthate among plant parts subsequent to its production is needed to fully understand behavior of vegetation in any ecosystem. The present study, undertaken primarily to obtain information on transport of assimilates into roots of desert vegetation, was conducted in the northern Mojave Desert, where the mean annual rainfall is about 10 cm. Shoots of *Ambrosia dumosa* (A. Gray) Payne plants were exposed to $^{14}\text{CO}_2$ in 1971, and the distribution of ^{14}C in roots, stems, and leaves was subsequently measured at 1 week, 2 months, and 5 months. Only about 12 percent of the ^{14}C photosynthate was stored in the root. Much of that stored in stems was available for new leaf growth. Photosynthate was labeled with ^{14}C for 24 plants representing eight species in 1972. Results showed that after 127 days the mean percentage of ^{14}C in roots as compared with the estimate of that originally fixed was 11.8; the percentage in stems was 43.8. The mean ratio of root to root plus stem for ^{14}C was 0.212, but this value was only half that of the ratio for actual weights of these parts of field plants. The correlation coefficient for $(^{14}\text{C in roots})/(^{14}\text{C in root + stem}) \times (\text{dry wt of root})/(\text{dry wt of root + stem})$ was +0.89. Small stems were the major storage organ for the ^{14}C . To check the validity of the ^{14}C data, root growth of eight perennial desert plants grown in the glasshouse was followed as plants increased in size. The mean percent of the whole plant that was root for eight species was 17.7 percent. The mean proportion of the increase in plant weights that went below ground for the eight species was 19.5 percent. This value is higher than the fraction of ^{14}C found below ground, and therefore the ^{14}C technique underestimates the movement of C to roots. Results of an experiment designed to test the value of the ^{14}C -pulse technique for determining current root growth for some perennial species from the desert indicated that the transition part of roots where root growth continued after exposure to ^{14}C was highly labeled. Old growth contained less ^{14}C than new growth.

The distribution of the products of photosynthesis among leaves, stems, roots, and reproductive parts must be understood if the dynamics of any plant community are to be known. Some data of this nature are available in the literature for desert plant species, but very little is quantitative (Cannon 1870, Dittmer 1964, Markle 1917). Jones and Hodgkinson (1970) give values for root and shoot weights of two *Atriplex* species. It is, of course, recognized that shoot-root ratios of plants and assimilate distribution vary with environmental conditions (Harris 1914, Kochenderfer 1973, Moore and West 1973, Wardlaw 1969).

The new photosynthate or assimilate in plants is subject to distribution among various plant parts, depending upon the phenological state. Such distribution is most likely under control of growth regulators

(Richmond and Lange 1957). As phenological events change, some of the assimilate will become redistributed (Schmer and Knievel 1972, Moser 1977). The sinks for such redistribution are often known (fruiting, leaf, stem, or root growth), but the sources are often obscure (leaf, stem, root, or other). In the case of redistribution prior to leaf abscission, the source is known, but the sinks are more obscure. The sources of assimilate for new growth following dormancy or defoliation from mechanical means (grazing, wind, harvest, etc.) are also obscure. Even when the plant part that constitutes the source is known, there remains the question of what really involves available carbohydrates or other assimilates.

Several ^{14}C techniques have been developed recently to study assimilate distribution in plants. The pulse technique (Caldwell et

¹Findings in this paper appeared, with several modifications, in The belowground ecosystem: a synthesis of plant-associated processes. Pages 303-310 in Range Science Department Science Series Report NA 26, Colorado State University, Fort Collins, 1977. We present these findings again for convenience and accessibility to readers interested in the several related papers in this volume.

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al. 1972, Wardlaw 1969), in which one or more foliar applications (pulses) of $^{14}\text{CO}_2$ are made and then two points of ^{14}C concentrations are looked for in the root systems, was partially evaluated under glasshouse conditions in the present study. The technique of foliar application of $^{14}\text{CO}_2$, in which gross distribution among leaves, stems, roots, and reproductive parts was measured (Gej 1972, Warembourg and Paul 1973, 1977), was also used. Techniques used elsewhere include foliar application of ^{14}C -urea (Clifford et al. 1973) and $^{14}\text{CO}_2$ labeling of specific leaves (Morooka and Kasai 1972). In the present study $^{14}\text{CO}_2$ was used to gain information on distribution of photosynthate and provide an estimate of annual primary productivity going below ground in perennial plants of a desert ecosystem.

MATERIALS AND METHODS

Photosynthate Distribution (^{14}C) in *Ambrosia dumosa* in 1971 in the Field

On 11 June 1971 about 0900, four *Ambrosia dumosa* (A. Gray) Payne plants in the northern Mojave Desert (1971 rainfall, 14.7 cm; 1972 rainfall, 11.8 cm) were covered with transparent plastic bags of 2 mil thickness, and 125 uCi $^{14}\text{CO}_2$ was released into each bag. Considerable water vapor condensed on the inside of the bags. Two hours later the bags were removed and leaf and stem samples were taken from each for determination by Q-gas counting of the amount of ^{14}C fixed. The technique for ^{14}C counting was that of Hendler (1959). All values were corrected to a sample size of 50 mg. Counting accuracy was made to a confidence level of 95 percent. The subsample of leaves and twigs was taken to represent between 5 and 10 percent of all those on the plant. A precise number of leaves was collected in each case, and an accurate estimate of those remaining on the plant was made so that a reasonably accurate assessment of the total ^{14}C fixed by the plants could be determined. Plants were excavated after 1 week, 2 months, and 5 months. Total ^{14}C present in

small roots, large roots, small stems, large stems, and leaves was determined.

Photosynthate Distribution (^{14}C) in Eight Plant Species in 1972 in the Field

On 21 March 1972 and 27 March 1972, 24 individual plants representing eight species, *A. dumosa*, *Atriplex confertifolia* (Torr. & Frem.) Wats., *Lycium andersonii* A. Gray, *Larrea tridentata* (Sesse & Moc. ex DC.) Cov., *Atriplex canescens* (Pursh) Nutt., *Ephedra nevadensis* Wats., *Lycium pallidum* Miers, and *Ceratoides lanata* (Pursh) J. T. Howell, were exposed to $^{14}\text{CO}_2$ each for 2 h in the field as in 1971. Ten mCi ^{14}C in NaHCO_3 were present in 200 ml solution and 5 ml was used for each plant. The $^{14}\text{CO}_2$ (250 uCi) was released inside the plastic bag by pouring HCl into the NaHCO_3 . After 126 to 127 days the plants were excavated and separated as before. At this time most of the leaves had abscised on the species which undergo summer dormancy.

Photosynthate Distribution Determined by Separation of Plants into Parts for Eight Plant Species Grown in a Glasshouse

Eight species of desert plants were propagated in the glasshouse in 1971, some by seedlings and others by cuttings, and planted individually into containers of Yolo loam soil (3.7 kg dry wt.). Nitrogen fertilizer (50 ug N/g as NH_4NO_3 monthly on dry weight of soil basis) was added, and the soil moisture tension was kept at around minus one-third bar during the study. The species employed were *A. canescens*, cuttings; *A. confertifolia*, cuttings; *Atriplex hymenelytra* (Torr.) Wats., cuttings; *E. nevadensis*, cuttings; *A. dumosa*, seedlings; *L. tridentata*, seedlings; *L. andersonii*, cuttings; *Lycium pallidum*, seedlings.

After about two months, individual plants were separated into leaves, stems, and roots at approximately two-week intervals to give a series of plants of different increasing sizes. Dry weights were determined, and the samples were counted for ^{14}C contents. The number of plants per species varied from six to eight replicates.

Evaluation of Pulse Technique for Measuring Root Growth

Glasshouse studies were undertaken in 1973 to evaluate the pulse technique (Wardlaw 1969) for measuring root growth following foliar fixation of ^{14}C . The idea is that a pulse of ^{14}C assimilate will be transported to the growing point of the roots and that this deposited ^{14}C mostly will not interchange with new assimilate being later transported to roots. Supposedly then, it would be possible to measure root growth extension from a given point in time by identifying that point with ^{14}C label. Also, it is believed possible that growth between two time intervals could be determined by using two separate pulses.

If roots produced annual growth rings, or if new assimilate exchanged with old materials, the technique would be of little value. To assess the utility of the pulse technique, plants were grown in solution culture with Hoagland nutrient solution. Eight species were grown in duplicate. These were *E. nevadensis*, *A. hymenelytra*, *Coleogyne ramosissima* Torr., *Atriplex cuneata* A. Nels., *Juncus mexicanus* Willd., *L. tridentata*, *L. pallidum*, and *A. dumosa*. Plastic bags were placed over the foliage and 5 μCi $^{14}\text{CO}_2$ was released into each. The roots were marked with black iron powder so that old and new root growth could be separated. After three weeks the amount of ^{14}C in new root growth in two increments as well as in other parts of the plants was determined by the procedures given above.

RESULTS AND DISCUSSION

Photosynthate Distribution (^{14}C) in *A. dumosa* in 1971 in the Field

In the 1971 ^{14}C -fixation study, the *A. dumosa* plants fixed about 4 percent of the ^{14}C supplied. Between the time of fixation and sampling dates, little of the ^{14}C seemed to have been lost to respiration because recovery after two months was around 90 percent of that originally fixed (Table 1). An interesting aspect of the data was the relatively low levels transferred to the roots (9.4 per-

cent at one week; 12.3 percent at two months; 10.0 percent at five months). This contrasts with 80 percent found for grasslands by Dahlman (1968), Singh and Coleman (1977), and Warembourg and Paul (1973, 1977). The very low level with *A. dumosa* may indicate that the newly fixed ^{14}C is entering a carbohydrate pool before transport to roots, under which conditions the label would underestimate the amount of translocation of photosynthate to roots because of dilution in the pool.

The leaves of *A. dumosa* seemed to serve as a storage sink for some time, but the major storage sinks were twigs and stems (Table 1). *Ambrosia dumosa* is a deciduous plant, so that photosynthate remaining in leaves is lost to the plant at the time of leaf abscission. Stored reserves in the stems become mobilized and are used in early development of new growth when environmental conditions become favorable. In *A. dumosa* the time of new growth development depends mainly on adequate soil water and is somewhat independent of temperature (Wallace and Romney 1972).

The transport of about 10 percent of the ^{14}C label below ground in fieldgrown plants contrasts with the 16.3 percent of new growth of the glasshouse plants compartmented in roots (see below). For solution culture (see also below) the root/root + stem for ^{14}C was 8.2 percent and for dry weight 28 percent.

In the plant sampled 5 months after labeling with ^{14}C , 56 percent of the estimated $^{14}\text{CO}_2$ fixed was still present in the plant (Table 1). In addition to respiration losses and losses from abscised leaves, there were losses due to flowering and fruiting and possibly also to consumption by herbivores. A portion (13.5 percent of the 56 percent) was present in new leaves that had grown in response to a late summer rain. At this point the root to root plus stem ratio for the ^{14}C was 20.7 percent, which is considerably less than for the weights of field plants (53.6 percent) (Wallace et al. 1974). One possible indication is that biomass losses from stems (animal, weather) are greater than losses from roots. Root to root and stem dry weight ratios of old plants then would be higher than the same ratio for ^{14}C measured after a short pe-

riod. As mentioned previously, the mixing of ^{14}C in a carbohydrate pool before translocation is another possibility.

Photosynthate Distribution (^{14}C)
in Eight Plant Species in 1972
in the Field

The 1972 data confirm the trend indicated by *A. dumosa* in the 1971 study (Table 2). In comparison with the estimated amount of ^{14}C originally fixed, the mean ^{14}C in roots for the eight species was 11.8 percent. It ranged from a low of 3.9 percent with *A. confertifolia* to a high of 22.3 percent for *L. pallidum*. These are the same species with low and high transport values for the glasshouse study (Table 3) and for root to root plus stem dry weight ratios from a field study (Wallace et al. 1974). The correlation coefficients for

the root to root and stem ratios for ^{14}C and the ratios of weights for field plants (Wallace et al. 1974) was +0.89. Again the ratios for ^{14}C are much below those for weight. The hypotheses mentioned above for *A. dumosa* presumably apply to all the other species studied. That is, in the field biomass loss is greater for stems than for roots so that the measured ratio is greater than the ratio of new photosynthate distributed between stems and roots. Also there may be some exchange between the labeled assimilate and older carbohydrates due to presence of pools, particularly for *A. confertifolia*, although a large proportion of this species is leaves and seed or flowers.

The transfer to roots of ^{14}C was especially low in those species which retained a high proportion of leaves at time of sampling. This was pronounced for *A. confertifolia*, *A. ca-*

TABLE 1. Distribution of ^{14}C label of photosynthate in plant parts of *A. dumosa* (1971).

	1 week	2 months	5 months
cpm fixed (2 h) ^a per plant	2,600,000	2,400,000	2,700,000
% remaining	98	90	56
	g dry wt/plant		
Leaves	18.77	9.54	3.96 ^b
Small stem	37.87	12.16	19.43
Large stem	27.99	42.97	25.12
Large roots	36.72	46.82	27.09
Small roots	6.33	8.02	6.38
	% distribution at sampling times of ^{14}C remaining in plant		
Leaves	57.0	22.2 ± 7.31	13.5 ^b
Small stem	25.7	35.4 ± 8.37	43.3
Large stem	7.7	28.8 ± 14.31	25.3
Large roots	8.5	10.4 ± 1.77	15.6
Small roots	1.1	3.2 ± 0.15	2.3
Total	100.0	100.0	100.0
	% of original fixed ^{14}C in stems and roots at sampling times		
Small stem	25.3	31.9 ± 7.5	24.2
Large stem	7.6	25.9 ± 12.9	14.2
Large roots	8.3	9.4 ± 1.6	8.7
Small roots	1.1	2.9 ± 0.14	1.3
Total roots	9.4	12.3	10.0
	^{14}C in stems/ ^{14}C in roots (ratio)		
	3.50	4.90	3.84
	^{14}C root/root + stem (%)		
	22.2	17.5	20.7

^a ± is plus or minus the standard deviation.

^bcpm fixed at 50 mg counting wt

^cOriginal leaves had abscised and a new flush of leaves had grown in response to late summer rain, but some of these leaves had abscised also.

rescens, *C. lanata*, and *L. tridentata*, in which the mean was 7.1 percent. The mean for ^{14}C found in roots for the other four species was 16.5 percent. The latter may be the more accurate estimate for distribution of new photosynthate below ground for the time period involved. Perhaps a longer time would be needed to evaluate root transport for the evergreen or near evergreen species. Also, temperature and soil water may change transport of assimilates (Schmer and Knievel 1972, Wardlaw 1969). Phenology conditions

may also induce transport to roots at later dates.

From the various studies made, it seems possible that only 10 to 20 percent (sometimes less) of the annual photosynthate goes into the root systems. Considering, however, that there are aboveground losses to respiration, herbivores, leaf abscission, wind, flowering, and fruiting, the estimates may be realistic. Net standing biomass of aboveground and below-ground structural plant parts is close to 2.5:1 (Wallace et al. 1980, this volume) in

TABLE 2. Distribution of ^{14}C label of photosynthate in parts of field-grown plants (1972) (after 126 or 127 days).

	Species							
	<i>Ambrosia dumosa</i>	<i>Atriplex confertifolia</i>	<i>Lycium pallidum</i>	<i>Lycium andersonii</i>	<i>Larrea tridentata</i>	<i>Atriplex canescens</i>	<i>Ceratoides lanata</i>	<i>Ephedra nevadensis</i>
Number of plants	4	4	4	2	2	2	3	3
^{14}C fixed in 2 h (10^6 Cpm/plant)	3.637	4.411	4.127	3.297	1.046	4.558	4.488	1.643
% remaining at sampling	63.5	86.6	66.2	66.5	77.6	78.5	78.2	90.4
	g dry wt/plant at sampling time							
Leaves	10.9	30.1	1.6	0.0	6.4	39.4	13.4	—
Large stems	48.5	15.8	18.7	22.3	3.2	39.7	11.8	—
Small stems	59.8	16.4	16.1	31.5	3.0	38.7	22.9	—
Roots	118.4	14.7	62.2	25.0	4.2	29.5	9.7	82.4
	^{14}C in plant parts at sampling (10^6 cpm/plant)							
Leaves	0.50	2.41	0.11	0.0	0.36	1.79	0.79	—
Stems	1.24	1.24	1.70	1.76	0.34	1.39	2.48	1.24
Roots	0.56	0.173	0.92	0.43	0.11	0.40	0.24	0.25
	Final distribution of ^{14}C in stems and roots (%)							
^{14}C fixed in 2 h (10^6 Cpm/plant)	20.3	19.7	23.3	17.4	26.5	38.9	15.3	16.2
Small stem	48.7	68.0	41.6	63.0	48.7	38.8	75.9	67.1
Large root	19.7	7.2	23.3	11.0	12.2	13.4	4.8	7.7
Small root	11.3	5.1	11.8	8.6	12.6	8.9	4.0	9.0
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
	^{14}C roots*							
^{14}C root + stem	0.310	0.122	0.351	0.196	0.244	0.224	0.087	0.168
	Percentage of original fixed ^{14}C in roots or stem at harvest time							
Stem	34.2	28.1	41.2	53.4	32.5	30.5	55.3	75.5
Roots	15.4	3.9	22.3	13.0	10.5	8.8	5.3	15.2

*Correlation coefficient of

$$\frac{^{14}\text{C in roots}}{^{14}\text{C in root + stem}} \times \frac{\text{g root}}{\text{g root + g stem}} \text{ in field} = +0.89.$$

spite of the low percentage of new assimilate going below ground. Small stems (twigs) may constitute the major storage site for carbon in these desert plants. The 1971 and 1972 years resulted in relatively little biomass production because of limited rainfall. This may affect the proportion of photosynthate being transported and stored in various plant organs and that lost through reproductive proportions being stored below ground.

Photosynthate Distribution Determined by Separation of Plants into Parts for Eight Plant Species Grown in a Glasshouse

In the glasshouse study on roots, the percentage increase in dry root weight compared with the percentage increase in total weight as plants increased in size indicated a mean percentage of new growth going below ground of 19.5 percent (Table 3). Highest value was for *L. pallidum* (33.7 percent) and lowest was for *A. confertifolia* (4.7 percent). In a companion field study with eight species, the highest root to root plus stem ratio was for *L. pallidum* (62.2 percent), and the lowest was for *A. confertifolia* (29.9 percent) (Wallace et al. 1974). The correlation coefficient between the ratios in Table 3 and the root to root plus stem ratio for the field (last column in Table 3) was + 0.98.

Evaluation of Pulse Technique for Measuring Root Growth

The results of the glasshouse ^{14}C studies of plants in solution culture revealed that the pulse technique (Wardlaw 1969) may have some value in providing an estimate of current root growth (Table 4). There was a hot spot at the transition zone where growth continued after the date of exposure to ^{14}C . The ^{14}C , at least for the three weeks of the study after exposure to $^{14}\text{CO}_2$, continued to be transported to the new roots. It is possible that this would not continue indefinitely, but even so there definitely would not be a completely sharp demarcation between roots grown before and after the date of labeling because both old and new growth contained ^{14}C . Carbohydrate pools, exchange among

carbohydrates, as well as root developmental biology must be better understood to evaluate such techniques. Caldwell et al. (1972) came to similar conclusions. The root/root + shoot ratio was generally much higher for dry matter than for ^{14}C (Table 4). This indicates that $^{14}\text{CO}_2$ may not be an accurate means of determining below-ground biomass.

CONCLUSIONS

The studies indicate that, as an average, somewhere around 10 to 20 percent of the carbon fixed by the perennial shrubs in the northern Mojave Desert was subsequently found below ground after a few months. Two different techniques gave close to the same results, although actual weighing of parts of plants grown under semicontrolled conditions gave higher values for transport to roots than did the ^{14}C procedure. Possible reasons for ^{14}C to underestimate the amount of below-ground transport may be the mixing of ^{14}C pools of carbon, so that the amount transported would be diluted in its content of ^{14}C and also the loss of roots in sampling.

The closeness of the two methods indicates that the proportion of the carbon fixed in photosynthesis in these woody plants that is transported below ground is much less than 50 percent, although for the standing biomass of these species 50 percent or more of it is below ground (Wallace et al. 1974). The differences, however, are not difficult to reconcile because the processes of respiration, flowering, fruiting, leaf abscission, harvesting by herbivores, etc., are constantly causing losses of carbon. In the Great Basin desert, Bjerregaard (1971) found much higher values for below-ground standing biomass than those found by us for the northern Mojave Desert. Grazing has occurred recently in that desert, however, but there has been no grazing in our study site for over three decades, and this may be an important factor in the differences.

Best answers for the questions of partitioning of photosynthate to below ground or to root, perhaps, can be obtained from field studies in which new seedlings are monitored for gas exchange (Koller 1970) for some years and for losses of carbon due to phenological

TABLE 3. Root, stem and leaf relationships for the plants grown in the glasshouse.

	No. of plants	Root	% distribution	
			Stem	Leaf
<i>A. dumosa</i>	9	20.5	44.4	35.1
<i>E. nevadensis</i>	10	14.5	85.5	—
<i>A. hymenelytra</i>	6	19.3	27.7	53.0
<i>A. confertifolia</i>	8	4.3	30.9	64.8
<i>A. canescens</i>	7	12.0	41.8	46.2
<i>L. pallidum</i>	9	26.3	59.3	14.4
<i>L. andersonii</i>	7	21.9	73.0	5.1
<i>L. tridentata</i>	7	23.5	39.6	36.9
Means		17.7		

*Calculated by using the smallest plant as the base.

**C.V. is coefficient of variation of $\frac{\text{root}}{\text{root} + \text{stem}}$

***Reference (Wallace et al. 1974).

events or harvesting. After several years the plants could be excavated and below-ground parts measured. If root losses due to soil fauna were minimal, then below-ground transport could be estimated fairly accurately for field conditions. Such experiments would be costly, however, and would require several years. We did a study slightly like this for 40 months (Wallace et al. 1980, this volume). The present estimates, although crude, perhaps would serve most purposes.

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Table 3 continued.

Mean increase dry wt in roots ^a	Root	Stem	Root		C.V. ^{**}	Root ^{***} root + stem (field data)
			root + stem			
% in root	g	g	%	SEM	%	%
% in whole plant						
26.4	5.33	10.43	33.8	3.01	26.7	53.6
13.2	1.03	6.08	14.5	0.68	14.8	45.5
19.5	4.52	6.47	41.1	2.57	15.3	—
4.7	1.19	8.59	12.2	1.66	38.4	29.9
12.7	3.15	11.77	21.1	2.01	25.2	40.2
33.7	5.74	12.91	30.8	1.96	19.1	62.2
20.9	6.56	19.20	25.5	2.72	28.1	45.5
25.0	4.78	8.07	37.2	2.94	20.9	55.3
19.5						

TABLE 4. Distribution of foliar absorbed ¹⁴C from plants grown in solution culture after new roots had developed three weeks after the ¹⁴CO₂ application.

Species	Leaf	Stem	Root old	Root transition ^o	Root new	Root root + stem
	cpm ¹⁴ C/g dry wt					ratio
<i>Ephedra nevadensis</i>	9880**	—	350	640	600	0.013
<i>Atriplex hymenelytra</i>	69120	9920	580	2780	1300	0.063
<i>Coleogyne ramosissima</i>	65520	8580	650	2280	800	0.073
<i>Atriplex cucata</i>	30360	28940	13840	34720	29000	0.352
<i>Juncus mexicanus</i>	15700**	—	7040	36940	18240	0.451
<i>Larrea tridentata</i>	28180	10240	2700	3040	2080	0.043
<i>Lycium pallidum</i>	43260	6440	1760	34400	34160	0.092
<i>Ambrosia dumosa</i>	20860	13140	1960	14820	7980	0.082
	g dry wt/plant part					
<i>Ephedra nevadensis</i>	17.42**	—	2.06	1.26	0.916	0.21
<i>Atriplex hymenelytra</i>	1.61	1.10	1.01	0.039	0.030	0.50
<i>Coleogyne ramosissima</i>	0.72	1.04	1.09	0.025	0.022	0.52
<i>Atriplex cucata</i>	1.79	0.63	0.56	0.031	0.037	0.50
<i>Juncus mexicanus</i>	9.02**	—	6.29	0.201	0.029	0.42
<i>Larrea tridentata</i>	3.29	7.95	1.06	0.202	0.089	0.15
<i>Lycium pallidum</i>	1.45	11.51	2.63	0.038	0.046	0.19
<i>Ambrosia dumosa</i>	4.33	5.28	1.85	0.132	0.081	0.28

*New root growth adjacent to the old.

**Mostly stem tissue.

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